Geographical Distribution of Diplopods in Great Britain and Ireland; Possible Causal Factors

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ABSTRACT

The locations and aspects of the habitats of Diplopoda have been recorded under the auspices of the BRITISH MYRIAPOD SURVEY Scheme since 1970 and records have been obtained from 1790 10 km squares of the British National Grid (Great Britain and islands) and 419 squares of the Irish National Grid (Ireland), a total now in excess of 30,000 species/location records. A provisional atlas was published in 1988 and a number of new records have increased our knowledge of the distribution of millipedes in these islands. The present report examines the pattern of distribution of species and the possible influence of climatic and other factors on the origins and distribution of the diplopod fauna. It is considered that a high proportion of the British and Irish fauna is likely to have arrived following the loss of the land connections with mainland Europe at the end of the last glaciation. Nevertheless there are considerable similarities with the fauna of nearby countries.

RÉSUMÉ

Répartition géographique des Diplopodes en Grande-Bretagne et en Irlande : les causes possibles.

Les localités et la nature des habitats des diplopodes des Îles Britanniques ont été répertoriées sous les auspices du BRITISH MYRIAPOD SURVEY, établissant un bilan depuis 1970 à partir de 1790 carrés de 10 km de côté, correspondant au carroyage national britannique UTM (Grande Bretagne et îles) et de 419 carrés correspondant au carroyage national irlandais UTM (Irlande). Le total des stations espèces/localités dépasse maintenant les 30 000. Un premier document a été publié en 1988 sous forme d'un atlas provisoire mais, depuis, un grand nombre de nouvelles données sont venues accroître notre connaissance sur l'inventaire et la répartition des espèces de diplopodes répertoriées dans les Îles Britanniques. Le présent travail aborde les modes de répartition des espèces, les influences possibles du climat ainsi que d'autres facteurs sur l'origine et la distribution biogéographique de la faune des diplopodes. On considère qu'une grande proportion de la faune britannique et irlandaise semble s'être constituée à la suite de la perte de continuité des terres émergées avec l'Europe continentale à la fin de la dernière glaciation. Il existe cependant de profondes similarités avec la faune des pays voisins du nord de l'Europe.

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INTRODUCTION

A distribution recording scheme for Diplopoda alongside one for Chilopoda was launched in 1970 by the BRITISH MYRIAPOD GROUP using an itemised record card which has been described elsewhere (BARBER & FAIRHURST, 1972). A new style card was introduced in 1985. The present review concentrates on the distributional data that has been derived from this.

The record card was designed for both professional and amateur usage and a very high proportion of records were in fact obtained by non-professional but highly competent recorders working in various parts of the British Isles. Identification was checked by a panel of referees as necessary so that the level of misidentification of specimens is likely to be insignificantly low.

By the nature of the scheme, the coverage was patchy.

1. At least initially, recorders tended to collect the larger and more conspicuous species. Smaller species and soil dwelling types will be under-recorded.

2. Some areas were recorded in great detail over many years (e.g. Yorkshire) whilst others had only one or a few casual collections made there.

3. Millipedes are highly sensitive to microclimatic changes and often seasonal in their occurrence so that a species may not be found on a particular occasion even though it is common in the area.

4. Different collecting procedures may yield quite different results. For instance, pitfall trapping generally collects the larger active iuliforms, polydesmids and *Chordeuma* spp.; finding *Stygioglomeris crinita* generally requires careful hand sieving of soil.

5. Immature specimens of some species e.g. *Polydesmus* spp. and *Chordeuma* spp. cannot be determined with accuracy. These may be the only specimens of a species found in a site.

There is a substantial element of chance in records being made. For instance BLOWER (1985) wrote, "There remains no evidence that *N. minutus* (= *venustus* in the sense of Schubart, 1934) has ever occurred in Britain, but there is a possibility that it may occur". It has subsequently (as *N. kochii*) been recorded on a number of occasions and is mapped from twelve 10 km grid squares.

RESULTS OF THE SURVEY

More than 400 individual recorders participated in the scheme and collections made for other purposes were also examined and a total of more than 30,000 species/site/data records are now held. This has allowed the plotting of distribution maps based on the British and Irish national grids using the 10 km square as the unit of recording. A preliminary atlas using the then available data was published in 1988 (BRITISH MYRIAPOD GROUP, 1988).

The present discussion is based on updated versions of these maps. Many more records were made in certain areas compared with others, often with much greater detail. Such well recorded areas include Kent, Surrey, Isle of Wight, Bedfordshire, parts of S. Wales, Yorkshire, Lothians, parts of Devon, Norfolk, Suffolk. Figure 1 shows the 10 km squares from which one or more records exist.

A summary of the regional distribution of species, including occurrence on outlying islands is shown in Table 1 and examples of distribution patterns are shown in Figures 7-18. An updated atlas of distribution will be published in due course, meanwhile records are held on cards and on the database at the Environmental Information Centre, Monks Wood, Huntingdon.

Nomenclature is as in BLOWER (1985) except that a new species, *Anthogona britannica*, is since described by GREGORY *et al.* (1994).

TABLE 1. — Distribution in various areas of the British Isles (X = presence in 1 or more 10 km grid square). Based on data from the MILLIPEDE SURVEY SCHEME. She = Shetland Islands, Ork = Orkney Islands, WIs = Western Isles, C&S = Caithness & Sutherland (North Scotland), Sco = Scotland, Ire = Ireland, IOM = Isle of Man, L&Y = Lancashire & Yorkshire, Sou = Southern England (South of line from Mersey - Wash, including SE and SW), Wal = Wales, SWE = South West England (Devon & Cornwall), KSS = Kent, Surrey, Sussex (extreme SE), CIs = Channel Islands (Jersey, Guernsey,etc,). NB: Shetland, Orkney, Western Isles, Caithness & Sutherland, Isle of Man and Channel Islands have relatively few records.

Species	She	Ork	WIs	C&S	Sco	Ire	IOM	L&Y	Sou	Wal	SWE	KSS	CIs
P. lagurus					X	X	X	X	X	X	X	X	X
G. marginata					X	X	X		X	X	X	X	
S. crinita					X	X		X	X	X		X	
A. gibbosa						X							
T. lobata									X				
P. germanicum									X			X	
C. rawlinsii					X	X		X	X	X	X	X	
N. polydesmoides		X	X	X	X	X	X	X	X	X	X		
B. melanops						X			X	X	X	X	
B. bagnalli/bradae						X		X	X				
C. silvestre									X		X		
C. proximum						X			X	X	X	X	X
M. gallica					X	X			X	X	X		
M. scutellare					X	X		X	X	X	X		
T. littoralis									X	X	X	X	
N. varicorne				X	X	X		X	X	X	X	X	
P. fuscus	X	X		X	X	X		X	X	X	X	X	X
C. palmatus					X	X		X	X	X	X	X	
N. kochii								X	X	X			
B. guttulatus					X	X	X	X	X	X	X	X	X
A. pallidus	X	X			X	X		X	X	X		X	
B. tenuis	X	X			X	X		X	X	X	X	X	
O. sabulosus				X	X	X	X	X	X	X	X	X	X
T. niger				X	X	X	X	X	X	X	X	X	X
A. nitidus					X	X		X	X		X	X	
C. londinensis					X	X			X	X		X	
C. caeruleocinctus					X	X		X	X	X	X	X	
C. vulnerarius						X		X	X	X	X	X	
C. latestriatus	X	X	X	X	X	X	X	X	X	X	X	X	
C. britannicus				X	X	X	X	X	X	X	X	X	
C. punctatus	X	X	X	X	X	X	X	X	X	X	X	X	
C. parisiorum						X		X	X	X	X	X	
C. truncorum									X			X	
E. armatus									X		X		
J. scandinavius				X	X	X	X	X	X	X	X	X	
O. pilosus				X	X	X	X	X	X	X	X	X	X
L. belgicus									X	X	X	X	X
L. kervillei									X		X	X	
M. pratensis									X			X	
B. pusillus				X	X	X	X	X	X	X	X	X	X
U. foetidus									X				
A. britannicus									X		X		
P. angustus		X	X	X	X	X	X	X	X	X	X	X	X
P. testaceus									X		X	X	
P. inconstans	X	X	X	X	X	X	X	X	X	X	X	X	
P. gallicus					X	X		X	X	X	X	X	
P. denticulatus	X			X	X	X		X	X	X	X	X	
B. superus		X	X	X	X	X	X	X	X	X	X	X	X
M. palicola					X	X		X	X	X	X	X	
O. albonanus					X	X		X	X	X	X	X	
S. italica						X			X	X		X	

DISTRIBUTION PATTERNS IN BRITAIN

Geographical

A crude analysis for the commonest species is displayed in Table 2. For the purpose of this, Great Britain is divided into a series of regions based on the 100 km grid squares (Fig. 2). For each species the total 10 km squares for that species is taken as a percentage of the total 10 km squares in that region for which records exist. This will underestimate smaller and more difficult to find forms and will also reflect the relative intensity of collecting. Thus, for instance, the northern part of Britain will have disproportionately more larger species recorded because much collecting there so far has been of a casual and superficial nature. For this reason, the values should be treated with great caution. Nevertheless they do show up the pronounced relative scarcity of *Ommatoiulus sabulosus* and *Julus scandinavius* in the southeast and an almost opposite pattern for *Cylindroiulus caeruleocinctus* which is relatively rarely found in the southwest. The north-south pattern of some species is also shown.

TABLE 2. — Analysis of records for the commonest species for regions of the British Isles as a percentage of total 10 km recorded squares for the region. NSco = Northern Scotland, SSNE = Southern Scotland & Northern England, MidE = Midland England, East = Eastern England, SEE = South East England, SWE = South West England, Wal = Wales, GBT = Total Great Britain, Ire = Ireland.

Species	NSco	SSNE	Y/L	MidE	East	SEE	SWE	Wal	GBT	Ire
P. lagurus									9.6	0.7
G. marginata	0.0	36.8	53.5	56.0	46.8	67.3	59.7	54.1	46.3	23.9
N. polydesmoides	9.2	27.4	55.1	46.0	51.7	55.6	38.1	45.2	40.1	32.5
C. proximum	0.0	0.5	0.0	1.3	0.5	9.3	8.3	42.6	6.0	0.2
N. varicorne	3.9	7.3	25.7	24.6	18.9	30.9	27.6	15.5	18.9	1.7
P. fuscus	27.5	36.8	58.3	41.9	57.9	47.8	54.6	55.8	47.6	18.1
B. guttulatus	2.4	9.4	21.9	38.2	24.4	34.6	25.4	27.7	23.0	11.3
O. sabulosus	32.7	29.9	34.8	23.9	32.3	5.9	28.2	30.4	26.9	4.8
T. niger	22.7	91.4	90.4	75.7	80.1	67.3	55.8	68.9	66.1	28.9
C. caeruleocinctus	4.8	5.3	4.9	18.4	17.9	33.7	5.0	2.7	11.1	0.2
C. punctatus	57.0	63.9	85.6	83.5	73.6	79.5	76.2	63.5	73.1	45.1
C. britannicus	5.3	13.5	17.6	22.3	7.0	19.0	9.4	20.2	14.6	10.0
J. scandinavius	23.7	28.8	49.7	32.0	34.8	6.8	54.1	47.3	33.4	6.9
O. pilosus	24.6	25.7	50.3	47.9	37.8	39.5	35.9	60.8	39.3	31.0
P. angustus	31.4	38.2	75.9	61.5	64.7	59.0	47.0	58.1	53.8	27.0
P. inconstans	6.8	8.7	12.3	10.7	11.4	15.6	3.3	2.7	9.3	6.7
P. gallicus	0.0	1.4	5.3	27.5	18.9	32.7	13.8	21.6	15.1	24.1
P. denticulatus	2.9	3.1	11.2	11.3	23.9	16.6	13.3	29.1	12.7	2.2
B. superus	8.2	16.3	32.1	31.1	43.3	54.0	42.0	27.0	30.9	10.0
M. palicola									8.4	0.7
O. albonanus									7.1	0.7

Species with a southeasterly distribution include *C. caeruleocinctus* (above) which may be increasing its range and *Stosatea italica* which is beginning to be found in a variety of areas in England, Wales and Ireland having been found fairly widely in East Kent originally, again presumably spreading, markedly synanthropic in many cases and found sporadically in rather superficial habitats. Also *Polydesmus testaceus* known only from Kent with one older Cornish record, *Metaiulus pratensis*, originally found in Kent and Sussex and recently found again in Kent, presumably mostly soil dwelling, *Polyzonium germanicum* mostly from Kent and *Cylindroiulus londinensis* often found around the London area, commonly in synanthropic sites but also recorded elsewhere in England.

Correspondingly, in the southwest *Enantiulus armatus*, so far found only in one area in Devon, *Chordeuma silvestre* from Cornwall, *Chordeuma proximum*, widespread in southwest

England, in much of the rest of southern England and very common in South Wales. The two *Leptoiulus* spp., *L. belgicus* and *L. kervillei* are typically southwestern but records across southern Britain are known and *L. belgicus* has been found in Ireland. Several species have not been found commonly in the southwest, if at all. These include *Archiboreoiulus pallidus*, *Craspedosoma rawlinsii*, *Cylindroiulus caeruleocinctus* and *C. londinensis*. *Brachychaeteuma melanops* is a distinctly southern species whilst the other two British *Brachychaeteuma* species seem to have a more central/northern tendency in general.

There is a distinct group of species apparently rare or possibly absent in northern Scotland. These include *Glomeris marginata*, *Brachychaeteuma* spp., *Chordeuma* spp., *Cylindroiulus caeruleocinctus, C. londinensis*, possibly *C. parisiorum, Blaniulus guttulatus, Choneiulus palmatus* and *Polyxenus lagurus*, although, especially given its distribution elsewhere in Europe, the latter may simply have been overlooked, something that may also be true of some other species listed. A number of species appear possibly to be absent from the Shetland Islands, etc. (Table 1).

Other factors

Apart from the fact that we do not really know the exact regional distribution of species, there are certain other factors which seem to affect where they are found. A frequently quoted influence is the presence of calcareous soils; in fact the number of species in Britain which show a clear calcicole tendency is quite small. *Stygioglomeris crinita* does appear to favour such soil; it may in fact be very widespread but the difficulty in finding it makes it impossible at the present time to be certain. *Stosatea italica* and possibly *Polydesmus testaceus* are also possible calcicoles. The other likely species restricted in this way is *Macrosternodesmus palicola*. *Cylindroiulus caeruleocinctus*, often found on calcareous soils, does not appear to be confined to them.

There are also a considerable number of species which favour agricultural and/or synanthropic sites. In the first category are possibly *Archiboreoiulus pallidus*, *Brachydesmus superus*, and maybe *Metaiulus pratensis*. Of the synanthropes many are also found elsewhere but they include *B. guttulatus*, *Brachychaeteuma* spp., *B. superus* (?), *Choneiulus palmatus* (?), *Cylindroiulus britannicus* (?), *C. londinensis*, *C. vulnerarius*, *C. truncorum*, *Nopoiulus kochii* (?), *Ophiodesmus albonanus*, *Polydesmus angustus* (?). *Thalassisobates littoralis* is a purely littoral species whilst *Cylindroiulus latestriatus* is a common coastal species but also found inland.

The very common *Cylindroiulus punctatus* is a distinct woodland species and is generally only found in woods, close to them or on the site of former woodland. Possibly other species show this tendency in a less pronounced form.

There are some species for which so few records exist that it is difficult to see a clear pattern. These include *Unciger foetidus* (one Norfolk site), *Anthogona britannica* (one Devon site, GREGORY *et. al.* , 1994, *Trachysphaera lobata* (Isle of Wight) and *Adenomeris gibbosa* (Dublin). Correspondingly there are species which seem to occur in a wide variety of habitats over a wide area. *Oxidus gracilis* and several other species are only known from glasshouses.

COMPARISON WITH OTHER AREAS IN EUROPE

Much of the British diplopod fauna is common with that of nearby areas of Western Europe. For some species, the British Isles seem to be the centre or one of the centres of their occurrence, a topic which is discussed by DOOGUE *et al.* (1993) with special reference to Ireland. Table 3 shows British species and their occurrence elsewhere on the continental mainland.

TABLE 3. — Distribution of species in various areas of Europe based on available information (X = presence out of doors). Based on DOOGUE *et al.* (1993), EASON (1970), ENGHOFF (1974 & pers. comm.), JEEKEL (1978), KIME (1990, 1992 and pers. comm.), LINDROTH (1957), MEIDELL (1972, 1979), MEIDELL & SOLHY (1979), PALMEN (1949), REMY & HOFFMANN (1959), etc. **U. foetidus* and *A. britannica* are known from single localities only in E and SW England respectively. Ice = Iceland, Fae = Faeroes, ShO = Shetland & Orkney, GBT = Great Britain, Ire = Ireland, Nor = Norway, Den = Denmark, NNW = North West Netherlands, NSW = South Netherlands, BeL = Belgium & Luxembourg, NFr = North France, Ame = Americas; var = various.

Species	Ice	Fae	ShO	GBT	Ire	Nor	Den	NNW	NSW	BeL	NFr	Ame
P. lagurus				X	X	X	X	X		X		
G. marginata				X	X	X	X	X	X	X	X	
S. crinita				X						X		
A. gibbosa					X							
T. lobata				X								
P. germanicum				X			X				X	
C. rawlinsii				X	X	X	X			X	X	
N. polydesmoides		X	X	X	X	X		X	X	X	X	
B. melanops				X	X							
B. bagnalli/bradae				X	X		X	X				
C. silvestre				X					X	X	X	
C. proximum				X	X						X	
M. gallica				X	X	X			X	X	X	
M. scutellare				X	X							
T. littoralis				X								
N. varicorne				X	X	X	X	X	X	X		
P. fuscus	X	?	X	X	X	X	X	X	X	X	X	X
C. palmatus				X	X	X	X	X	X	X		X
N. kochii				X		X	X	X	X	X		X
B. guttulatus	?			X	X	X	X	X	X	X		X
A. pallidus		X	X	X	X	X			X			
B. tenuis			X	X	X	X	X	X	X	X		
O. sabulosus				X	X	X	X	X	X	X	X	
T. niger				X	X			X	X	X	X	
A. nitidus				X			X	X	X	X	X	
C. londinensis				X	X	X					X	
C. caeruleocinctus				X	X		X	X	X	X		X
C. vulnerarius				X	X			X	X	X		
C. latestriatus		X	X	X	X	X	X	X	X	X		
C. britannicus				X	X	X	X	X				X
C. punctatus			X	X	X	X	X	X	X	X	X	X
C. parisiorum				X	X		X	X		X	X	
C. truncorum				X			X	X	X	X	X	X
E. armatus				X								
J. scandinavius				X	X	X	X	X	X	X	X	
O. pilosus				X	X	X	X	X				
L. belgicus				X	X				X	X	X	
L. kervillei				X					X	X	X	
M. pratensis				X								
B. pusillus				X	X		X	X	X	X		X
U. foetidus				*		X	X	X				
A. britannica				*								
P. angustus			X	X	X	X	X	X	X	X	X	
P. testaceus				X					X	X	X	
P. inconstans	X		X	X	X	X	X	X	X	X	X	X
P. gallicus				X	X					X		
P. denticulatus				X	X	X	X	X	X	X		X
B. superus	X	X	X	X	X	X	X	X	X	X	X	X
M. palicola				X	X		X	X	X	X		
O. albonanus				X	X		X	X	X	X		X
S. italica				X	X			X	X			
Other species						3	9	5	4	16	var	

Almost all species recorded from Norway occur in Britain with the exception of *Polydesmus complanatus* (Britain has *P. angustus*) and *Leptoiulus proximus* but a number of British species have not yet been found there. Eastern Fennoscandia similarly has a high proportion of "British" species (PALMEN, 1949) but with other more eastern ones. Denmark, with 37 outdoor species, includes 9 not found as yet in Britain. The Netherlands has a somewhat similar fauna to eastern Britain, several not found in Britain, with southeast Netherlands having several species only found in southern Britain. Data for Belgium, Luxembourg and northern France shows most British forms although species such as *Adenomeris gibbosa*, *Trachysphaera lobata*, *Enantiulus armatus* and *Metaiulus pratensis* seem to come from further south. There are about 16 species from the Belgium, Luxembourg area which do not occur in Britain as far as is known as present.

KIME (1990) has mapped a number of species in Europe and has demonstrated some curious aspects of this such as the disjunct distribution of *Ophyiulus pilosus* with a seeming gap in its occurrence between Britain and Scandinavia/North Germany/Poland and Bavaria/Italy. He demonstrates *Nanogona polydesmoides* as Britain/France, *Chordeuma proximum* similarly but *C. silvestre* (only here known from Cornwall) with a much wider occurrence. It would be helpful to have more data from northern France for comparative purposes.

POSSIBLE CAUSAL FACTORS IN DISTRIBUTION

Present Day Climate

The climate of the British Isles is usually described as Atlantic or Oceanic with comparatively low temperatures in summer and comparatively high in winter compared with nearby continental Europe. But within this description is considerable local variation, including the influence of the sea in coastal areas, altitude in so called "Highland Britain" (mostly western and northern areas) and the "heat island" effect of urban areas which may permit the survival of species outside their normal range.

Mean annual rainfall varies from below 500 mm in part of Eastern England to more than 1600 mm in areas of the west and up to more than 2400 mm in some mountainous areas, with a general tendency for much of mid-southern, southwestern and northwestern England together with Wales and Scotland to have 800 mm or more, as does Ireland (Fig. 3). Given the sensitivity of myriapods to moisture one might seek some correlation with this but there is no obvious one for most species except perhaps, in England and Wales, *Chordeuma proximum*.

Temperature is frequently a factor influencing animal distribution, affecting as it may do survival for individuals, availability of food and breeding cycles. High summer (July) isotherms tend to run in an approximately east-west direction (Fig. 5) and there are a number of species referred to which appear either to have a southerly distribution or are, as in the case for instance of *Glomeris marginata*, absent from apparently suitable habitats in northern areas of Scotland. Until more data is available on the effect of temperature on breeding cycles etc. in diplopods one can only speculate on the causal factors here.

DAVID (see this volume) describes how *G. marginata* in an oak forest in southern France tends to move into the soil in winter, confirming previous work that suggests that it is in fact cold intolerant. SUSTR (see this volume) describes how *G. marginata* has a much lower metabolic rate than *G. balcanica* and *G. hexasticha* at low temperatures, which may mean that in cold conditions it is unable to assimilate effectively and would therefore be unable to tolerate these conditions for any length of time.

January mean isotherms (Fig. 4) tend to run in a more north-south direction with the western areas relatively warmed by the influence of the sea whilst the eastern parts have a more "continental" colder drier climate. There do not appear to be clear correlations with species here but the more extreme, drier climate of the south-east, especially Kent, may favour, either directly or by excluding competitors, certain species such as *Polyzonium germanicum*, *Stosatea italica*, *Polydesmus testaceus*, and *Metaiulus pratensis*.

Past Climates and Land Bridges

Conditions during the Devensian (Würm) glaciation were such that much of the British Isles were covered with ice sheets, reaching at their maximum the whole of the area north of South Wales and North Yorkshire and the Norfolk coast. At the same time mainland Britain was joined both to Ireland and to mainland Europe by land bridges. The area south of the ice sheets was subject to periglacial conditions. Under such circumstances, the diplopod fauna was likely to have been extremely sparse if not entirely absent in the present day area of the British Isles. Sub-arctic conditions would have prevailed down to about 10,000 BP following the climatic improvement of the Aller interstadial. A temperature with a July mean below +10 is quoted for this Younger Dryas phase (NILSSON, 1982). This period was then followed by the transition to Pre-Boreal and the re-establishment of forests. VAN DER HAMEN *et al.* (1971) describe conditions as having reached mixed deciduous oak forest in the Netherlands by 8,000 BP.

Such conditions would clearly favour the spread of species north from climatic refuges. However, rising sea levels led to the breaking through at the Dover Straits about 9,600 BP and between East Anglia and the Netherlands in 8,600 BP (JONES, 1985). After this period the only dispersal across the English Channel/North Sea would be by passive transport or human activity. There is thus a period of about 400-1400 years during which species could re-invade Britain directly. However, the effective separation of Ireland must be placed earlier and this has been considered to account for the absence in that country of some species of animals (e.g. certain amphibians and reptiles) present on mainland Britain.

A number of species of diplopod do occur in fairly northern locations in Europe. PALMEN (1949) reported *Proteroiulus fuscus* north of latitude 66 degrees with *Cylindroiulus latestriatus* and *Ommatoiulus sabulosus* north of 64 degrees and *Polyxenus lagurus*, *Polydesmus denticulatus* and *Polyzonium germanicum* all north of 62 degrees in Eastern Fennoscandia. MEIDELL (1972) included *P. lagurus*, *P. fuscus*, *Polydesmus complanatus* (which does not occur in Britain), *C. latestriatus* and two species usually regarded as synanthropes in northern Europe, *Blaniulus guttulatus* and *Cylindroiulus londinensis* as his most northerly recorded species. EASON (1970) reports three species, *Brachydesmus superus*, *Polydesmus coriaceus* and *P. fuscus* with possibly *B. guttulatus* from Iceland. These latter must have all presumably arrived in some way from other parts of Europe but their existence in Iceland indicates a degree of tolerance of local conditions there.

GOLOVATCH (1992) in his survey of the Russian Plain describes *P. fuscus* from tundra, *P. fuscus, P. germanicum* and two other species from northern taiga; these plus *P. lagurus, O. sabulosus* and five other species from mid taiga, and amongst species from southern taiga, *P. denticulatus* and *N. varicorne*.

FIG. 1. — 10 km grid square distribution: total records for the British Isles.

FIG. 2 . — Regions used for Table 2 analysis.

FIG. 3. — British Isles: Mean Annual Rainfall in mm (based on ATKINSON & SMITHSON *in* CHANDLER & GREGORY, 1976).

FIG. 4. — British Isles: Mean January Temperatures 1941 - 70 (reduced to sea level) (after TOUT *in* CHANDLER & GREGORY, 1976).

FIG. 5. — British Isles: Mean July Temperatures 1941 - 70 (reduced to sea level) (after TOUT *in* CHANDLER & GREGORY, 1976).

FIG. 6. — British Isles: Fig of the Main Devensian ice advance (solid line) (after SPARKS & WEST, *in* EVANS, 1975).


1
2
SHETLAND
ORKNEY
IRELAND
WALES
EAST
3
800
>800 mm
<800 mm
4
5
6

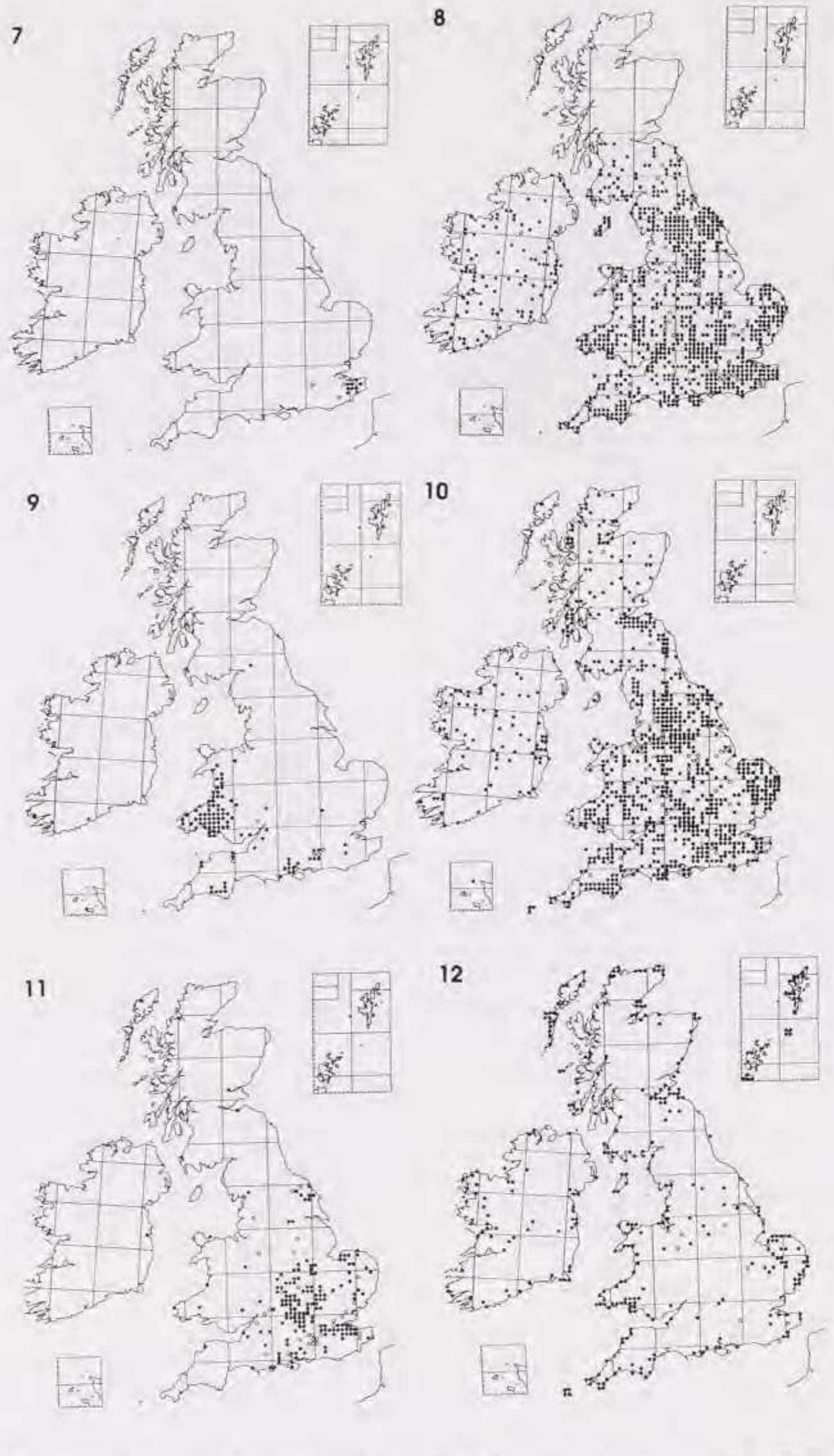

FIG. 7-18. — 10 km distribution Figs of selected species: 7. *Polyzonium germanicum*, 8. *Glomeris marginata*, 9. *Chordeuma proximum*, 10. *Proteroiulus fuscus*, 11. *Cylindroiulus caeruleocinctus*, 12. *C. latestriatus*, 13. *C. londinensis*, 14. *C. punctatus*, 15. *Julus scandinavius*, 16. *Ophyiulus pilosus*, 17. *Leptoiulus kervillei*, 18. *Enantiulus armatus*.

13

14

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Clearly there is therefore a possibility of some of the above species being able to tolerate conditions in southern Britain during glacial times or at least to cross the land bridge before it broke down. Most of these species are widespread in both Britain and Ireland (although, for some reason, *P. germanicum* is confined to the extreme southeast).

Once the land bridges had broken, then entry to the British Isles was possible only by either passive transport by rafting or by being brought in accidentally by human activity. Rafting is not easy to demonstrate although PALMEN (1949) refers to *P. fuscus* on driftwood in S. Finland and suggest that such passive transport combined with parthenogenesis could account for its occurrence on outlying islands.

Evidence for possible entry of animals via land bridges or survival during periglacial conditions is provided by reptiles and amphibians, especially the latter which would be highly vulnerable to salt water. These animals are of sufficient size that the likelihood of accidental transport by human activity will be far less than that for soil invertebrates such as diplopods. Six reptiles and the same number of amphibians are recorded from the British isles together with two recent successful introductions, *Rana esculenta* and *R. ridibunda*. These latter, together with the fact that other species have occurred in the past (HOLMAN, 1993), suggest that it is historical factors that have determined the relative paucity of British species. Of the British forms, only 1 reptile and 3 amphibians occur in Ireland. One of these, *Bufo calamita* seems somewhat anomalous and has been a field for some speculation (see, e.g. BEBEE, 1984). The lower number of species fits in with the idea of an earlier isolation of Ireland. Of the species that do occur these all occur in Scandinavia (ARNOLD & BURTON, 1978) with *Lacerta vivipara* and *Rana temporaria* extending to the extreme north and *Triturus vulgaris* to mid Norway/Sweden. *Bufo sp.*, *R. temporaria*, *L. vivipara* and the widespread British snake *Natrix natrix* are known from Devensian deposits.

Given that the present herpetological fauna was in place by about 8,800 BP (HOLMAN, 1993), by which time separation would have been occurring, we could visualise that a relatively small number of diplopod species, derived from adjacent areas of Europe, was already present. These might have included *Polyxenus lagurus*, *Proteroiulus fuscus*, *Nemasoma varicorne*, *Ommatoiulus sabulosus*, *Cylindroiulus latestriatus*, *Polydesmus denticulatus* and others.

Other species would arrive either by rafting on tree trunks or other material or be brought in accidentally with plant material or soil by human activity (see below).

Whatever the mode of their arrival, the improvement in climate towards the so-called Climatic Optimum of about 7,000 - 5,000 BP, when mean temperatures were about 2-3 degrees higher than at present, would have covered much of the country. Subsequent climatic changes such as the climatic oscillation around 5,500 - 5,000 BP and the so called "Little Ice Age" AD1550 - 1850 may well have brought about later contractions in range. The patchy distribution one now sees for instance of species widespread in France such as *Enantiulus armatus* and the *Leptoiulus* spp. could be vestiges of a once wider occurrence.

Entry by Rafting and Human Influence

It is difficult to give convincing evidence for rafting by organisms such as millipedes but it has certainly been suggested for a variety of animal types for oceanic crossing (see for instance, GARDNER, 1985 referring to geckos in the Seychelles and Mascarenes). Littoral or coastal species (such as *Cylindroiulus latestriatus*, a very widespread island species) are most easily transported in this way and parthenogenesis as in the case of *Proteroiulus fuscus* would assist. However, a variety of species from woodland might be transported as a result of exceptional conditions e.g. storm damage in coastal areas.

Human influence has undoubtedly assisted in the spread of some species of recent arrival such as *Cylindroiulus vulnerarius* and human introduction of invertebrates to islands is widely quoted (see e.g. JONES & PRATLEY, 1987). Human activity undoubtedly plays a part in the spread of soil animals. A recent example is the New Zealand planarian, *Artioposthia triangulata* in Britain (J. FREW, pers. comm.) first recorded in Scotland in 1965 but with 416 records by 1992.

The occurrence of myriapods in isolated islands such as Iceland as well as the islands around Britain or those of Denmark (ENGHOFF, 1974) are best explained in terms of transport either by rafting or human influence. The very high proportion of British species in Ireland, where land connection would have been lost soon after the disappearance of the ice, cannot be convincingly explained by reference solely to land bridges but must involve transport across water.

LINDROTH (1957) has listed 17 species of diplopod known from Europe which occur in the Americas, 16 of which (including *Oxidus gracilis*, a greenhouse form of tropical origin) are found in Britain. Of the 18 species of millipede reported from Newfoundland 16 are regarded as introduced forms from Europe with 37 of the 42 isopods and myriapods falling into this category. Clearly such species have been introduced by human influence and presumably could have reached the British Isles in the same way. LINDROTH gives five criteria for an introduced species; it is difficult to apply these to the present situation except for very clearly recent arrivals or species with clearly synanthropic habits such as *Cylindroiulus vulnerarius* or *C. truncorum*. If glacial and periglacial conditions and subsequent breakdown of land bridges had left a number of vacant niches then presumably these could be filled by incoming species with the appropriate characteristics. It is difficult to conceive of common species of woodland and other habitats such as *Glomeris marginata* and *Tachypodoiulus niger* as other than "native" species. In this case then opportunities for crossing the land bridge in the wake of the ice must have been rather greater than we have suggested.

Cylindroiulus londinensis, common in much of France, is an example of what may be an "old" introduction which has or is still spreading out from the London area, largely in synanthropic or semi-synanthropic areas.

CONCLUSIONS

We would suggest that a fairly high proportion of British diplopods are likely to be forms which may have arrived in the period after the breakdown of the land bridges between Britain and Ireland and between mainland Europe and Britain. Although climatic and other conditions are not identical with nearby areas the fauna is similar apart from some more eastern and southern species, and the occurrence of species both on islands and in America confirms their ability to cross water. There are likely to have been subsequent changes in distribution due to climatic changes, the introduction of new species, habitat destruction and possibly to other as yet imperfectly understood factors, such as those quoted by FORD (1982) for butterflies.

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REFERENCES

ARNOLD, E. N. & BURTON, J. A., 1978. — *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. London, Collins. 242 pp.

BARBER, A. D. & FAIRHURST, C. P., 1974. — A habitat and distribution recording scheme for Myriapoda and other invertebrates. *Symp. Zool. Soc. Lond.*, **32** : 611-619.

BEBEE, T. J. C., 1984. — Possible Origins of Irish natterjack toads (*Bufo calamita*). *Brit. J. Herpetology*, **6** : 398-401.

BLOWER, J. G., 1985. — *Millipedes* (Synopses of the Br. Fauna NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

BRITISH MYRIAPOD GROUP, 1988. — *Preliminary Atlas of the Millipedes of the British Isles*. Huntingdon, NERC. 65 pp.

CHANDLER, T. J. & GREGORY, S., 1976. — *The Climate of the British Isles*. London/New York, Longmans. 390 pp.

DOOGUE, D., FAIRHURST, C. P., HARDING, P. T.& JONES, R. E., 1993. — A Review of Irish Millipedes (Diplopoda). *In* : M. S. COSTELLO, *Biogeography of Ireland: past, present and future. Occ. Publ. Ir. biogeog. Soc.* **2**.

EASON, E. H., 1970. — The Chilopoda and Diplopoda of Iceland. *Ent. scand.*, **1** : 47-54.

ENGHOFF, H., 1974. — Om tusindbenenes udbredelse i Danmark (Diplododa). *Ent. Meddr.*, **42** : 21-32.

EVANS, J. G., 1975. — *The Environment of Early Man in the British Isles*. London, Unwin. 216 pp.

FORD, J. J., 1982. — *The Changing Climate: Responses of the Natural Flora and Fauna*. London, Allen & Unwin. 190 pp.

GARDNER, A. S., 1985. — Viability of the eggs of the day-gecko *Phelsuma sundbergi* in sea water. *Brit. J. Herpetology*, **6** : 435-436.

GOLOVATCH, S. I., 1992. — Some patterns in the Distribution and Origin of the Millipede Fauna of the Russian Plain (Diplopoda). *Ber. nat.-med. Verein Innsbruck*, **510** : 373-378.

GREGORY, S. J., JONES, R. E. & MAURIÈS, J. P., 1994. — A new species of Millipede (Myriapoda, Diplopoda, Chordeumatida) from the British Isles. *J. nat. Hist.*, **28**, 1993 : 47-52.

HOLMAN, J. A., 1993. — British Quaternary herpetofaunas: a history of adaptations to Pleistocene disruptions. *Herpetological J.*, **3** : 1-7.

JEEKEL, C. A. W., 1978. — Voorlopige atlas van de verspreiding der Nederlandse Miljoenpoten (Diplopoda). *Verslagen technische Gegevens Inst. taxon. zool. Univ. Amsterdam*, **15** : 1-69.

JONES, D. K. C., 1985. — Shaping the Land: The Geomorphological Background. *In* : S. R. J. WOODELL, *The English Landscape, Past, Present, and Future*. Oxford, Oxford University Press.

JONES, R. E. & PRATLEY, P., 1987. — Myriapods of the Isles of Scilly. *Bull. Br. Myriapod Group.*, **4** : 7-15.

KIME, R. D., 1990. — *Fauna Europaea Evertebrata: A Provisional Atlas of European Myriapods Part 1*. Luxembourg, European Invertebrate Survey. 109 pp.

KIME, R. D., 1992. — On Abundance of West European Millipedes (Diplopoda). *Ber. nat.-med, Verein Innsbruck*, **510** : 393-399.

LINDROTH, C. H., 1957. — *The Faunal Connections between Europe and North America*. New York/Stockholm, Wiley/Almqvist & Wiskell, 326 pp.

MEIDELL, B. A., 1972. — En faunistisk undorsokelse avyte Harangerfjordens myriapod fauna og en oversikt over norske myriapoders taxonomiske og dyregografiske status. Thesis, Bergen, University of Bergen (Maps given *in* The distribution of Norwegian myriapods as known to 1972 with a revised list of published papers devoted to the same subject. Zool. Museum, University of Bergen.

MEIDELL, B. A., 1979. — Norvegian Myriapods: Some Zoogeographical Remarks. *In* : M. CAMATINI, M. *Myriapod Biology*. London, Academic Press : 195-202.

MEIDELL, B. A. & SOLHY, T., 1979. — Terrestrial Invertebrates of the Faroe Islands:VI Centipedes and Millipedes (Chilopoda and Diplopoda). *In* : A. MINELLI, *Proceedings of the 7th International Congress of Myriapodology*. Leiden, Brill. : 413-427.

NILSSON, T., 1982. — *The Pleistocene*. Dordrecht/Boston/London, Reidel. 651 pp.

PALMEN, E., 1949. — The Diplopoda of Eastern Fennoscandia. *Ann. Zool. Soc. "Vanamo"*, **13** : 1-54.

REMY, P. & HOFFMANN, J., 1959. — Faune des Myriapodes du Grand-Duché de Luxembourg. *Arch. Sect. Sci. Inst Gr. Ducal Luxembourg*, **26** : 199-236.

VAN DER HAMEN, T., WIJMSTRA, T. A. & ZAGWIJN, W. H., 1971. — Floral Record of the Late Cenozoic in Europe. *In* : K. K. TUREKION, *The Late Cenozoic Glacial Ages*, Newhaven, Yale University. Press. 606 pp.